THE INTRAMUSCULAR ENDINGS OF FIBERS IN THE SKELETAL MUSCLES OF THE DOMESTIC AND LABORATORY ANIMALS.

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It may be said that muscular fibers in skeletal muscles are of three general forms—the cylindrical, which extend from tendon to tendon, as in the shortest muscles, and in penniform muscles; the conical, with one end at a tendon, the other tapering to a point within the muscle, and the spindleform, with both ends tapering to a point within the muscle. The two latter forms, the conical and spindleform, occur in most long skeletal muscles which are not penniform.

In a previous paper * it was shown that conical and spindleform fibers occur in the longer muscles of minute animals, and the form and relations of the endings were figured. As that paper had a full bibliography, only a few titles will be given with the present paper.

It is the object of the present paper to consider the occurrence of intramuscular ends, and to show their exact form in the skeletal muscles of animals used for dissection and experiment.

The animals examined are carp (Cyprinus carpio), necturus (Necturus maculatus), frog (Rana catesbiana and R. virescens), snapping turtle (Chelydra serpentina), hen (Gallus domesticus), duck (Anas boschas), and English sparrow (Passer domesticus), among the immammalia; opossum (Didelphys virginiana), white rat (Mus ——), mouse (Mus musculus and Hesperomys leucopus), rabbit (Lepus cuniculus), mole shrew (Blarina brevicauda), sheep (Ovis aries), cow (Bos taurus), bat (Vespertilio subulatus, Atalapha cine-

* Form, endings, and relations of striated musclar fibers in the muscles of minute animals (mouse, shrew, bat, and English sparrow). Susanna P. Gage. The Microscope, 1888, pp. 225–237 and 257–272, 5 plates, and in abstract in the Proceedings of this Society for 1887.

reus, Atalapha noveboracensis), raccoon (Procyon lotor), kinkajou (Cercoleptes caudivolvulus), dog (Canis familiaris, three varieties, coach, terrier, and spitz), and cat (Felis domestica), among the mammalia.

In each animal as long muscles as possible were chosen, as the *latissimus dorsi*, *biceps femoris*, or *sartorius*, or in the necturus and carp, the respiratory muscles of the throat.

The best practical method for preparing large numbers of slides is that fully described in the proceedings of this Society for 1889, pp. 34–45. In brief, the muscle is dissociated in 20 per cent. nitric acid until the connective tissue is softened, washed in water, dissected in picro-glycerin, and mounted in glycerin jelly, or, after washing with water, the muscle may be kept indefinitely in a saturated solution of alum water containing 2½ per cent. of chloral hydrate. It may then at any time be mounted in glycerin jelly or in Canada balsam.

The careful examination of the intramuscular ends found in this way show that, though there is great diversity of form, several types may be distinguished. There are simple tapering forms, such as are usually described (Fig. 1). These may have a long slender taper of 3 to 7 millimeters, ending in a mere filament, or they may terminate more abruptly in a somewhat brush-like form.

There are also tapering ends which branch; these may be subdivided into four varieties: 1st, the end of the fibers divides into two nearly equal parts, both striated (Fig. 2); 2d, a striated branch is given off at some distance from the tip of the fiber (Fig. 14); 3d, several striated branches are given off at varying distances along the side of the tapering end, the last branch occurring 3 to 8 mm. from the tip of the fiber, at a point where the fiber becomes of full size (Fig. 4); 4th, unstriated projections are given off along the side of the fiber; these may be mere filaments or projections of greater thickness (Figs. 6 and 7).

In the different forms of vertebrates studied there is considerable difference in the occurrence of these types.

In the carp, frog, and necturus the great majority of fibers in the longer muscles extend from tendon to tendon. Even in a sartorius 7 cm. long, taken from a gigantic bullfrog (Rana catesbiana), this is the case. These fibers have a variation in diameter not observed in any of the higher animals when it was certain that the fibers were not tapering to a point. Some of the fibers have only ⅛th to $\frac{1}{10}$th

the diameter of others, and without great care one might suppose them to be tapering ends. The frog and necturus, however, undoubtedly have a few fibers which taper to intramuscular ends. The case is much more doubtful in the respiratory muscles of the carp, the longest ones found in that fish. These results differ somewhat from those of other authors. It has been stated that in the frog's *sartorius* the fibers all extend from tendon to tendon. Rollett* says that intramuscular tapering ends are found in the frog and carp. Herzig and Biesiadecki† say that dichotomously divided ends are found in the *gastrocnemius* of frog and the body muscles of *Lota vulgaris*. Further examination is necessary to harmonize or explain these differences.

In the snapping turtle tapering ends are numerous, but no departure from the simple unbranched type was found.

In birds, the hen, duck, and sparrow, numerous tapering ends with a long gradual taper were found. A few of them were divided near the tip into two parts (Fig. 2), and a still smaller number showed branchings of other types (Fig. 3).

In mammals, as in birds, the majority of endings are of the simple, tapering form, but in every species examined there was also a varying proportion of branched endings. In some cases, as the cat, they are rare, except in the diaphragm (Fig. 18); in others, as the mouse, they are comparatively common. The size of the branches varies so greatly that in some cases high magnification (Fig. 19) and great care are necessary for their detection; in others they are patent with a low magnification. In the opossum (Fig. 4) and rodents (Fig. 13) it may be said that the endings have many and large branches, while with the cow (Figs. 9 and 10) and the cat (Fig. 19) the branches are few and small.

As to the particular form of branching in any species, no generalization can at present be made. In most of the species several forms are found more or less like the above types. The figures show a few of the more remarkable endings found in the different species and are selected with the view of showing the diversity of forms occurring.

Other authors have found branched endings in the skeletal muscles of some of the mammals, as Herzig and Beisiadecki, l. c., in the

* Sitzungsb. d. k. Akad. d. Wissench. Math-naturw. Cl. Wien, Bd. XXXI, 1856, heft I und iii, pp. 176–180, 1 pl.

† Die verschiedenen Formen der quergestreiften Muskelfasern. Sitzungsb. d. k. Akad. d. Wissench. Math-naturw. Cl. Wien, 1858, pp. 146–149, 3 pl.

horse; Krause,* in the ocular muscles of the cat; Tergast,† in the ocular muscles of the sheep; Gage,‡ in the cat and rat, and Felix,|| in man and the rabbit.

These statements summarized show that tapering intramuscular ends are common in vertebrates. A few cases are recorded of branched endings in frogs and fishes. These need corroboration. They certainly occur in three widely separated species of birds and in eight of the fifteen orders into which Claus divides the mammals, and in species so widely separated as the opossum and man.

It may safely be predicted that sufficiently careful examination will prove that branched intramuscular ends occur in at least some of the longer muscles of all mammals and birds.

No one factor has yet been discovered which accounts for the usefulness of this branching and its greater development in some species than in others. Neither the comparative activity nor the size of species seems to account for the differences; for the cow and cat have few branches, the opossum and mouse many. Its phylogenetic significance appears to be slight; for, though below birds it is at least rare, it is marked in the lower mammals, while among the higher mammals, the nearly allied cat and dog show a great difference, the cat having few branches, the dog many.

The general occurrence of such branched ends demands an investigation of the mode and time of their development. The appearances in the fully formed fiber and the fact that a nucleus is generally found in the angle formed by a branch lead to the conclusions that a growth of the fiber takes place at the intramuscular end; that the fibrils of which it is composed do not advance at equal pace, and a nucleus formed at the periphery of one fibril may prove the obstacle which turns the adjacent, oncoming fibril from its course, and that thus arises a distinct branch.

A few observations upon a fœtal opossum, a fœtal calf (Fig. 11), and a calf a few weeks old (Fig. 12) give the impression that when the stage is passed when all fibers extend from tendon to tendon,

* Handbuch der menschlichen Anatomie. Band I, s. 81, Hannover, 1876.

† Ueber das Verhaltniss von Nerven und Muskel, Arch. für mikr. Anat., Bd. IX, 1873, pp. 36–46, 1 pl.

‡ Muscular tissue. Reference Handbook of Medical Sciences, Vol. V, pp. 59–74, illustrated. New York, 1887.

|| Die Länge der Muskelfaser bei dem Menschen und einigen Säugetheiren. Leipzig, 1887, pp. 1–9, 1 Fig. From the "Festschrift für Albert von Kölliker."

fibers are formed which have simple tapering ends; with increase in diameter, some of these become branched.

If this view of the formation of fibers be correct, the sarcolemma can hardly be a preformed sac, but must be a growing deposition either from the fiber itself or the surrounding connective tissue. This agrees with Beale's statement that the sarcolemma is absent in the branching fibers of the tongue, &c.*

The fringed appearance of the extreme end of fibers and their branches, first mentioned in a previous paper (l. c.), seems to be rather more a gradual tapering of the individual fibrils with a loss of striation than a distinctly tendinous structure, although a similar appearance in insect muscle has since been interpreted by van Gehuchten† as a transition to tendon. This appearance was seen in most of the forms examined, but was well marked wherever the tips were comparatively wide, as in opossum (Fig. 4) and rabbit (Fig. 13).

However important these purely morphological points, the physiological side seems still more so. How do these tapering ends join other fibers in order best to execute their work of contraction? From the study of the specimens it seems that no one mode is universal. A tapering end may be closely cemented to a fiber from the same or the opposite direction, and either to a tapering end or a fiber at full size; or, in some cases, it may have a continuation of clear connective tissue which extends on into the general intramuscular connective tissue. Branching ends join other fibers more or less closely, in some cases forming anastomoses with other branching ends, as in the mouse.

In the rat (Fig. 8) and opossum anastomoses were found between two fibers, while in the rabbit, bat, and shrew the indications are strong that fibers unite by the tips of the fringed branches. On these points further investigation is necessary. Such anastomoses occur in the alimentary canal of invertebrates and the iris of birds, while in skeletal muscles Tergast (l. c.), has found them in the ocular muscles of sheep, and Felix says they occur in man.

The close connection of fibers mentioned above should be taken into consideration in any physiological experiments on the transition of a nervous impulse from one fiber to another.

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* On the structure and formation of the sarcolemma of striped muscle, and the exact relations of the nerves and vessels to the contractile tissue of muscle. Trans. Royal Micr. Soc., 1864, pp. 94–108, 2 pl.

† Verhandl. Anat. Gesellschaft, 1889, pp. 100–105.

Summary.

1. In cold-blooded vertebrates many fibers extend from tendon to tendon of the longest muscles, and thus exceed the assumed maximal limit of 4 cm. A few simple tapering intramuscular ends were found in the frog and necturus; none were found in the carp, but many in the turtle.

2. In the longer muscles of the birds and mammals examined most of the fibers end intramuscularly, either by simple tapering ends or by branched ends of varying form. Probably branched ends will be found in the longer muscles of all adult warm-blooded animals.

3. The development of the tapering fibers demands complete investigation, especially with reference to the branched ends. It appears that at first there are no branches, but that they arise by an unequal growth of the fibrils at the tip of a fiber.

4. The branching ends appear to have very close connection with other fibers, in some cases anastomoses occurring. This must have a bearing upon the question of the transmission of a nervous impulse from one fiber to another.

Description of Plate.

Intramuscular ends of fibers from long muscles of the domestic and laboratory animals. The examples were chosen from a great number of drawings to show the diversity of form occurring, though no one can be called typical in any species. The drawings were made with Abbé's camera lucida at a magnification of about 250 diameters.

Fig. 1. A typical, simple, tapering end, such as is found in varying numbers in the necturus and frog and all the birds and mammals examined.

Fig. 2. An ending from a long muscle on the ventral side of the neck of a duck (Anas boschas). The end is dichotomously divided at the tip. This type is found more frequently in birds than in mammals.

Fig. 3. From the *biceps femoris* of a hen (Gallus domesticus), with branches at some distance from the tip. This type is somewhat infrequent in birds.

Fig. 4. From the *trapezius* of an opossum (Didelphys virginiana), with large, strongly marked, spreading branches at the tip and along the side of the fiber to the point where the fiber becomes of full size. This is a remarkably large, well-

marked example of a type which is found in greater or less abundance in all the mammals examined, with perhaps the exception of the cow, cf. Figs. 13 and 15.

Fig. 5. From the *sartorius* of the opossum, with several compressed branches. A type not frequent, cf. Fig. 9.

Figs. 6 and 7. From the *biceps femoris* of a white rat (mus), showing unstriated branches. The peculiar fringed appearance in Fig. 7 is quite rare, cf. Fig. 19.

Fig. 8. The anastomosis of two fibers from the *biceps femoris* of the white rat.

Fig. 9. From the *psoas* and Fig. 10 from the *latissimus* of a cow (Bos taurus). Compared with the size of the endings, the branches are small and compressed, while few fibers were found on which branchcs occur. Endings like Fig. 10 were found in no other animal.

Fig. 11. From the *sartorius* of a fœtal calf about one half meter long. No branched ends were found.

Fig. 12. From the *latissimus* of a calf five or six weeks old. A few simple branching ends were found, the branches being larger in proportion to the end than in the adult. The comparative diameter of the endings in Figs. 11, 12, 9, and 10 is noticeable.

Fig. 13. From the *biceps femoris* of a rabbit (Lepus cuniculus). This type is frequent, though other less branched forms are found.

Fig. 14. From the *latissimus* of the sheep (Ovis aries). Branched ends are frequent.

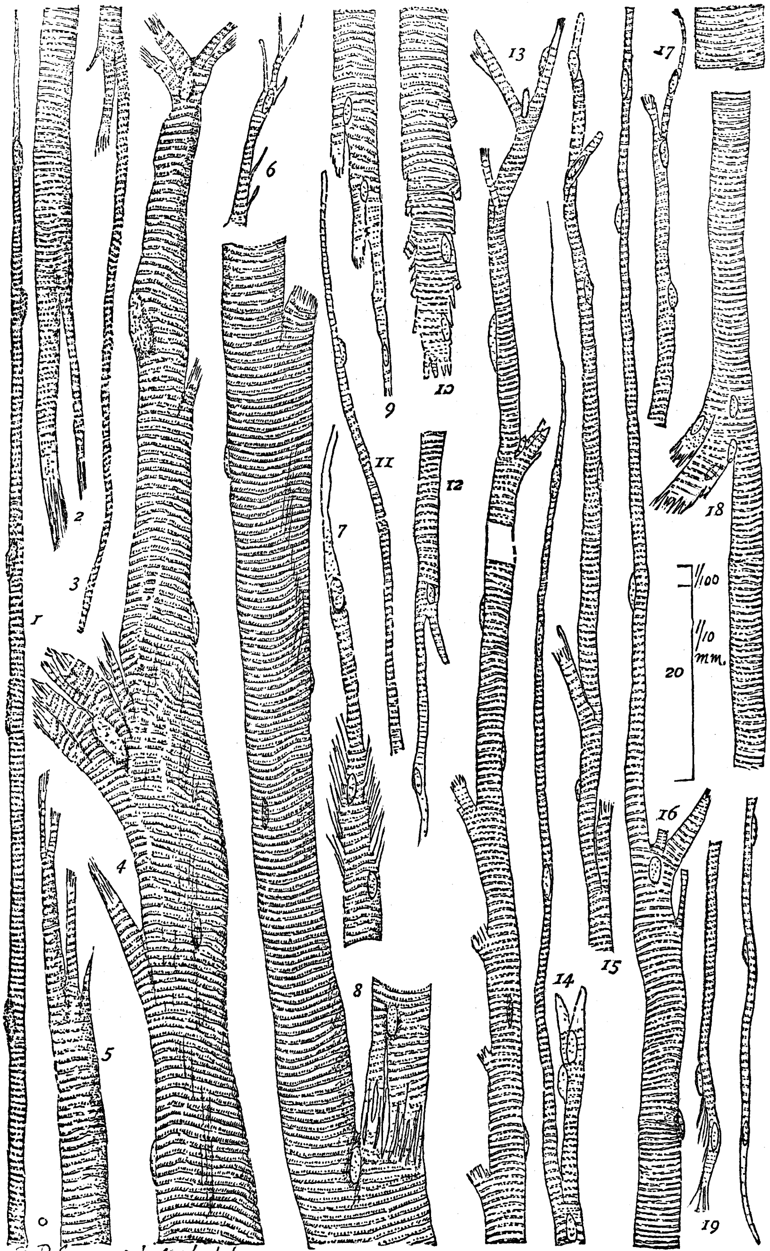
Fig. 15. From the *latissmus* and Fig. 17 from the *sartorius* of a small dog (Canis familiaris) (terrier).

Fig. 16. From the *latissmus* of a large coach dog. This is an unusual form, though branches are frequent.

Fig. 18. From the diaphragm of a half-grown kitten (Felis domestica). Several much-branched forms were found in this muscle.

Fig. 19. From a brachial muscle of the cat (Felis domestica). Striated branches in the ordinary skeletal muscles seem to be rare in the cat.

Fig. 20. Scale of $\frac{1}{100}$ or $\frac{1}{10}$ mm. magnified the same amount as the drawings of the plate.



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